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REPORT

Assessment of Blue Mussel *Mytilus edulis* Fisheries and Waterbird Shellfish-predator Management in the Danish Wadden Sea

Karsten Laursen, Per Sand Kristensen, Preben Clausen

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Abstract We assessed the blue mussel *Mytilus edulis* fishery management scheme introduced in 1994 in the Danish Wadden Sea that regulate fishing vessels, fishery quota, set-aside for mussel-eating birds and established zones closed to mussel fishery. The results showed (i) a reduction in the blue mussel biomass and mussel bed areas in zones closed to fishery, (ii) decrease in eiders *Somateria mollissima* numbers and increase or stable numbers for oystercatcher *Haematopus ostralegus* and herring gull *Larus argentatus* and (iii) that energy estimations based on ecological food requirements for the mussel-eating birds should be at least three times larger, than the amount set-aside in the mussel management scheme. It is concluded that the mussel management scheme had been unable to stabilize or increase the blue mussel stocks and to secure stable or increasing numbers for all target bird species. Thus, it is recommended to revise the present blue mussel management scheme in the Danish Wadden Sea, to continue and improve mussel stock and bird surveys, and to consider novel studies of the mussel-eating birds' energetics for improved set-aside estimates and future assessments.

Keywords Biomass · Ecological food demand · Eider · Favourable conservation status · Herring gull · Natura-2000 · Oystercatcher · Wadden Sea

INTRODUCTION

The Wadden Sea contains the largest tidal flats in the world and is shared between the Netherlands, Germany and Denmark (Paulin and Kent 2001). It is of global international importance as a breeding, staging and wintering area to over fifty populations of migratory waterbird species (Scott and Rose 1996; Dettmann and Enemark 2009; Delany et al. 2009). Accordingly, all three countries have designated the majority of the Wadden Sea as wetlands of international importance under the Ramsar Convention and as Natura 2000 areas under the EU Birds and Habitats Directives. Despite these conservation designations, sympathetic management, high public and scientific awareness, continued exploitation of shellfish in estuarine and tidal habitats by both fishermen and bird species poses particular challenges for a successful fisheries management within protected areas. Human exploitation of shellfish, combined with natural causes (such as severe winter weather) can reduce shellfish stocks upon which waterbirds rely (Dankers and Beukema 1983; Atkinson et al. 2003). Collapse of shellfisheries has been reported from both Britain, Denmark and the Netherlands (Dare et al. 2004; Dahl et al. 1994; Ens 2006) and depletion of shellfish stocks due to natural events and/or overexploitation by fisheries have caused large scale emigration amongst oystercatcher *Haematopus ostralegus*, reduction of body condition and mass mortality in eider *Somateria mollissima,* and affected survival in knot *Calidris canutus* (Atkinson et al. 2003; Camphuysen et al. 2002; Gils et al. 2006; Laursen et al. 2009).

Endeavours to establish sustainable use of natural resources, as required by the Convention on Biodiversity since 1992 and the EU Habitats Directive since 1993, led to the adoption of novel conservation policies in the countries sharing the Wadden Sea during the 1990s with the aim of regulating human exploitation of shellfish populations. Although the management policies in the three countries differ, they all include, or have included, regulation of vessel numbers, annual fishing quotas, establishment of areas closed to blue mussel, common cockle *Cerastoderma edule* and surfclam *Spisula* spp. fishing, and the establishment of food reserve stocks for birds (Essink et al. 2005).

This report focuses on the management of blue mussel *Mytilus edulis* fishery and of waterbirds feeding on mussels in the Danish Wadden Sea. The introduction of management mechanisms to regulate the mussel fishery was the response to an intensive and unregulated blue mussel fishery (involving up to 40 vessels) that developed during 1984 to 1988. This, in combination with three severe winters in the mid-1980s, caused a collapse in blue mussel stocks by 1988 (Dahl et al. 1994). Follow this collapse, measures were taken to re-establish blue mussel stocks by regulating the mussel fishery, with the objectives of re-establishing sustainable human exploitation while securing sufficient food for the three most numerous mussel-eating birds: eiders, oystercatchers and herring gulls *Larus argentatus*. The first and immediate response to the 1988 collapse of mussel stocks was a general ban, which closed the Danish Wadden Sea to blue mussel fishery in 1989–1990. Between 1990 and 1993, blue mussel fishing was only allowed on an experimental basis in a small area of Grådyb (Dahl et al. 1994). From 1994 onwards, a new mussel management scheme was put in place by the Ministry of Fisheries, permanently reducing the number of fishing licences to five vessels and closing c. 48% of the Danish Wadden Sea to blue mussel fishing (Fig. 1). At least 50% of the estimated mussel production (and not less than 10,300 metric tonnes) was allocated to mussel-eating birds. The scheme permitted that if the remaining mussel stock exceeded that reserved for the birds, an annual quota was given to the fishermen based on regular monitoring of the blue mussel stocks and production estimations (Kristensen and Borgstrøm 2005).

The aim of this article is first to assess the effectiveness of the blue mussel management scheme since it was brought into force in 1994. As indicators of success, we assume that the scheme should secure (i) sustainable blue mussel stocks, (ii) a sustainable blue mussel catch for the fishermen, (iii) sufficient food for the mussel-eating birds, and (iv) increases in mussel stocks and numbers of mussel-eating birds in zones closed to mussel fishery. To test the efficacy of the measures, we used a before-after control-impact (BACI) design (Bro et al. 2004) and sought to demonstrate that (i) blue mussel biomass has increased since the collapse in 1988, (ii) blue mussel bed areas, mussel biomass and mussel-eating bird numbers had increased since the mussel management scheme was put into force in 1994, (iii) annual mussel landings had increased since 1994 and (iv) mussel stocks and mussel-eating bird numbers had increased in zones closed to mussel fishery. Second, we present new calculations for estimating the food demands of waterbirds feeding on mussels which are based on a combination of physiological, energetical, and ecological considerations relevant to mussel-eating birds, and using current best practice modelling based on energetic demands (Ens et al. 2004; Goss-Custard et al. 2004).

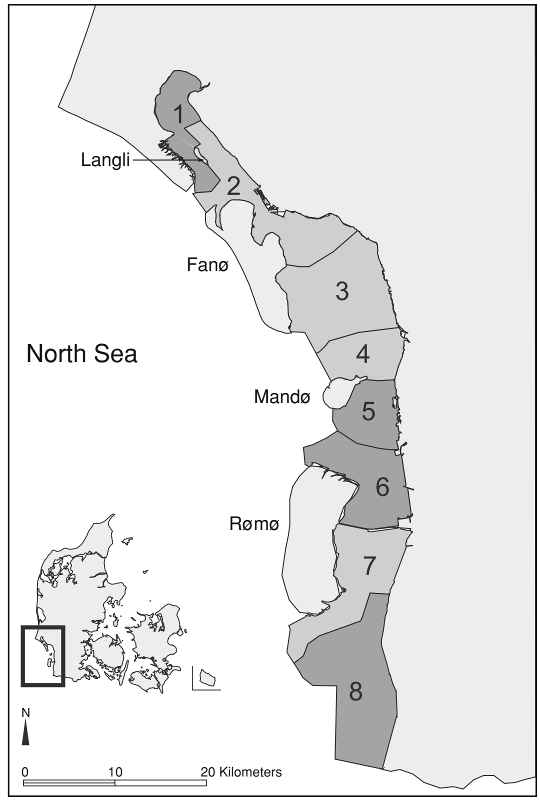

Fig. 1 Map of the Danish Wadden Sea showing the positions and size of zones 1–8. The blue mussel management scheme was introduced in 1994 allowing blue mussel fishery in zones 2, 3, 4, and 7 (*light grey*), whereas zones 1, 5, 6 and 8 were permanently closed to mussel fishery (*dark grey*). Parts of zone 1 between the island, Langli and the peninsula to the west, has been designated an ecological reference area since 1982 with no human (and mussel fishing) activity

STUDY SITE

The Danish Wadden Sea forms the northern c. 10% of the Wadden Sea. The area was designated a Special Protection Area for birds (SPA) under the EU Birds Directive in 1983, as a Ramsar site in 1987, and a Special Area of Conservation (SAC) under the EU Habitats Directive in 1998. According to the current national designation criteria, the SPA supports internationally important populations of 21 waterbird species, including eiders and oystercatchers, as well as several bird species mentioned in Annex 1 of the EU Birds Directive, and habitats and species mentioned in the Annexes of the EU Habitats Directive (Agency for Spatial and Environmental Planning 2009).

For this study the Danish part of the Wadden Sea between the mainland and the offshore islands was divided into 8 zones (numbered 1–8) of which four zones were open and four zones were closed to mussel fishery after 1994 (Fig. 1). Blue mussel beds are situated along the gullies and the deeps, as well as in littoral and sub-littoral beds between the islands and the mainland coast. In the Danish Wadden Sea only naturally occurring wild blue mussels are fished, artificial mussel lots are not permitted, so no fishery for seed mussels take place.

BLUE MUSSEL AND BIRD SURVEYS

Mussels

Since 1986, blue mussel stocks have been monitored in September–October by compiling information on (i) mussel bed area measured from digitised aerial photographs every second or fourth year, and assuming bed areas were constant between photographical surveys (for more information, see Kristensen and Borgstrøm 2005); (ii) tidal mussel biomass, by ground sampling from exposed beds, collecting mussels in plots of 0.25 m^2 and estimating mussel coverage to establish the relationship between dense mussel clusters and open areas without mussels to give the total extent of cover within inter-tidal mussels beds; supplemented by between 18 and 63 dredge samples in zone 2 covering around 22 km^2 of the sub-tidal area in every 1 to 2 years (average area per dredge sample 400 m^2, range 11–2,607 m^2); (iii) sub-tidal mussel biomass using a commercial mussel dredge, dividing catch biomass weight by the dredged area, multiplied by catching efficiency to estimate the actual mussel density. Subsamples were taken for measuring shell lengths. Shell size distributions for each tidal basin were estimated, and length-weight relationships were calculated using the formula: $W = 0.09076 * L^{2.973726}$, where W is the total weight in grams (shells included), and L the shell length in mm (Kristensen and Borgstrøm 2005). Annual production was calculated as half the total biomass (Munch-Petersen and Kristensen 2001). Based on the annual blue mussel production calculated for a given year, a quota for the mussel fishery was established after setting aside 10,300 metric tonnes for the mussel-eating birds (see later). Data for mussel bed area and biomass are provided for 6 of the 8 zones; data for zones 5 and 6 were pooled and data from zone 4 and 8 were few, and were therefore excluded from the calculations. Estimations of sub-tidal mussel bed areas were changed from 2004 and onwards, thus we can only compare size of mussel bed areas between years up to and including 2004.

Information on the amounts of landed blue mussels was obtained from the Danish Fishery Directory.

Waterbirds

In total 209 aerial surveys were performed during 1980–2008 covering the Danish Wadden Sea. From 1980–1996 surveys were conducted almost monthly (176 surveys), whereas during 1997–2008 only 1–3 annual surveys (33 surveys) were carried out, but always including a mid-winter survey when eiders are found in high numbers. Two observers in the aircraft identified and estimated the bird species abundance and distributions. The aircraft flew at c. 130 km h^{-1} and at c. 60 m altitude. Surveys only took place on days with visibility >5 km, wind speed <25 km h^{-1} and no rain. Surveys were carried out at high tide following the same route every time, and using the 'total count' method of surveying water birds from aircraft (Pihl and Frikke 1992). Aerial surveys of waterbirds were used in order to cover the whole area in one operation of less than 4 h duration, rather than using very time-consuming land-based surveys (which give a poor coverage of mudflats and tidal channels far away from land). It is evident from a comparative study, that differences in counting efficiency from aircraft, compared to expectedly more accurate ground counts, was small for the focal species, i.e. eider numbers counted from aircraft only deviated 1.1 ± 19.0% (mean ± SE) from land counts, oystercatcher 4.7 ± 9.9% and herring gulls 10.5 ± 10.0% (Laursen et al. 2008). The large SE values indicate relative large differences in counted numbers from the two platforms when considering each specific count. On the other hand, the small mean values show that the differences in numbers between the two platforms become close to each other when more counts are included. This indicates that the differences in counted numbers are not caused by numbers counted from one of the platforms only. When comparing bird numbers in zones open and closed to fishery, we corrected for difference in area size.

SET-ASIDE CALCULATIONS FOR MUSSEL-EATING BIRDS

1994-Version (Physiological Food Demand)

In the 1994 mussel management scheme set-aside for mussel-eating birds were 10,300 metric tonnes TWW (total wet weight) (eiders 8,875 tonnes, oystercatcher 980 tonnes, herring gull 445 tonnes) (Kristensen and Borgstrøm 2005). The 10,300 tonnes had been arrived by: (i) estimating the number of bird-days spent by eiders, oystercatchers and herring gulls per year in the Danish Wadden Sea, where bird-day numbers had been calculated from mean monthly numbers recorded from aerial surveys conducted during 1986-1999, multiplied by the number of days each month, and summed by year, and these computations led to the following estimates: for eiders 5.2 million bird-days $year^{-1}$, oystercatchers 6.5 million bird-days $year^{-1}$ and for herring gulls 5.3 million bird-days $year^{-1}$; (ii) assuming that eiders subsisted on 60% blue mussels in their diet, oystercatcher 17% and herring gull 5%; (iii) applying estimates of physiological daily energy expenditure and daily food consumption necessary to cover the normal daily energetic demands on the three bird species (oystercatcher: on average 45 g AFDW of mussel meat per day; herring gull: on average 91 g AFDW of mussel meat per day; and eider: on average 160 g AFDW of mussel meat per day) (Kristensen and Borgstrøm 2005).

These initial calculations of the amount of mussel biomass to be set-aside followed the same principles as Hilgerloh (1997), but they neglected to include elevated thermoregulatory costs during cold periods, nor did they take account of the fact that some mussels will be inaccessible to feeding birds (e.g. covered by other mussels or in waters too deep for feeding birds), energetically unfavourable to eat (if too small, handling times and energetic costs associated with feeding will exceed the energetic benefit) or impossible to eat (mussels too large). Recent studies demonstrate that such constraints are essential to take into account when considering the proportion of accessible prey in relation to energetic and food consumption issues in mussel-eating birds (e.g. Goss-Custard et al. 2004, Nehls, G. 1995, de Leeuw et al. 1999).

2008-Version (Ecological Food Demand)

Following a European Court Judgment in 2004 (European Court 2004), the Danish Forest and Nature Agency (Ministry of Environment) demanded more extensive Environmental Impact Assessments before the fishing authorities could grant annual quota for fishing vessels in the Wadden Sea. Inter-ministerial consultations involved with this process in 2008 led to re-evaluation of the methods used to calculate the quantities of mussels that have to be set-aside for mussel feeding birds before catch quota could be granted. The Danish Agency for Spatial and Environmental Planning (Ministry of the Environment) thus recommended that computations should be based on bird numbers counted in the years 1980–1985, and that computations should be based on the average of annual maxima for these years. This period includes the date when the EU Birds Directive was enforced, and is prior to the overexploitation of mussels by fisheries and declines in eider numbers. We thus considered the average of annual maxima as a target number of birds, assigned this number to the month with highest numbers (for eider in February, oystercatcher in November), and estimated similar target numbers for the two species in all other months based on proportional computations. The target numbers and monthly bird-days computed this way are approximately similar to 90% percentiles of monthly means for both species. For herring gull, which is not a designated species in the SPA, we used average monthly mean counts for the computations. The novel computations gave for eiders 6.7 million bird-days $year^{-1}$, for oystercatcher 9.3 million bird-days $year^{-1}$ and for herring gull 5.2 million bird-days $year^{-1}$ (see Table 2).

In the revised food demand calculations we used the same figures on the proportion of blue mussels in the bird species' diet (eider 60%, oystercatcher 17% and herring gull 5%) as previously used (Kristensen and Borgstrøm 2005).

The daily energy expenditure (DEE) of the birds were estimated from the birds basal metabolism (BMR) multiplied by factors that should correct for increased thermoregulatory energy expenditure caused by cold air (oystercatcher) or water (eiders), and for eiders also energy used to maintain the salt concentration in the body. BMR for eiders and herring gulls were calculated from the allometric formula given by Lasiewski and Dawson (1967) for non-passerines, using body weights from Cramp and Simmons (1977, 1983), and for oystercatchers we used values from Stillman et al. (2000). DEE for eiders were calculated as 3.0 * BMR in months when water temperature was more than 15°C (May–October) and as 4.3 * BMR when it was less than 15°C (Nehls 1995). DEE for oystercatchers were calculated according to the formulae given by Stillman et al. (2000), which correct for an increasing energy demand of 31.8 kJ day^{-1} for every degree that the air temperature drops below 10°C. In absence of species specific data for herring gulls, their DEE was calculated as the average value of estimates given by Drent et al., Walsberg and Nagy (Ebbinge and Weijand 1978; Walsberg 1983; Nagy 1987).

The energy content of mussel meat was assumed to be 22 kJ g^{-1} ash-free dry weight (AFDW) (McLusky 1989), and the formula AFDW = 0.055 * TWW was used to calculate from AFDW to total wet weight (TWW) (including shells) (Munch-Petersen and Kristensen 2001), i.e. energy content of whole mussels equate to 1,21 kJ g^{-1} TWW.

Birds can not extract all the energy available from their food intake, and digestion efficiency was estimated at 75% for the eiders, which swallow whole mussels (Nehls 1995) and 85.4% for oystercatchers, which pick out the flesh from the mussel shells (Stillman et al. 2000). The latter figure was also used for herring gulls, although the species has mixed feeding patterns: swallowing whole mussels, cracking larger shells by dropping them, and acting as a kleptoparasite.

Goss-Custard et al. (2004) estimated an ecological food requirement (EFR) for oystercatchers as 2.5–7.7 times more than the estimated food requirements needed to fulfil their food demand during winter, based on field data from five estuaries in Western Europe, and argued for the use of a similar factor for Eiders. The EFR takes into account that bird species can not remove all flesh from inside the shells, that parts of the mussels are stolen by gulls and that the mussels have flesh losses during winter due to respiration (and nearly no assimilation). In this study, we use the low value (2.5) for eiders, since we think that the intra-specific competition during feeding is low and the species swallow the mussels whole, restricting losses. For oystercatcher we use the high value (7.7), as this was specifically found for oystercatchers feeding on blue mussels in other studies (Goss-Custard et al. 2004). For the herring gull, which has different feeding strategies, the average value (5.46) of estimates given by Goss-Custard et al. (2004) was used.

RESULTS

Blue Mussel Data, Comparison Before and After 1994

In zones 1, 5 and 6 (which were closed to the mussel fishery after 1994) the average mussel bed area estimated for the three zones pooled declined from >6.41 km^2 in 1986–1993 to 3.35 km^2 in 1994–2000 (Table 1) ($P < 0.05$; $N_{7,14}$. Wilcoxon two-sample test). On the other hand, in the zones open to the mussel fishery (no. 2, 3 and 7) the average extent of the beds has not changes between the two periods (4.32 km^2 versus 5.70 km^2, data pooled) ($P > 0.05$; $N_{12,20}$. Wilcoxon two-sample test).

The total annual amount of estimated blue mussel biomass in the Danish Wadden Sea varied considerably during 1986–2007 (Fig. 2). The biomass was estimated at 40,000 metric tonnes in 1986 and it increased to a maximum of 117,000 metric tonnes in 1994 thereafter it gradually decreased to less than 12,000 metric tonnes since 2003. There was no statistical change in the total biomass before and after 1994 ($P = 0.529$; $Z = 0.65$; $N_{8,14}$. Wilcoxon two-sample test). Biomass data is only available for zone 1 (closed to mussel fishery) and zone 2 (open to fishery), and although large biomass changes had occurred in both zones no statistical changes were found before and after 1994 in either of the zones ($P > 0.05$; $N_{4,10}$. Wilcoxon two-sample tests).

Blue Mussel Data, Analyses After 1994

The total mussel biomass estimated in the Danish Wadden Sea decreased significantly after 1994 (Fig. 2) ($P < 0.001$; $T = -4.44$; DFE = 12, regression analyses with autoregressive errors). From 1994 to 2007, the blue mussel biomass was annually estimated for five zones, two zones closed and three zones open to fishery. In all five zones, annual estimated biomass decreased during the period, and the pooled biomasses for zones closed and open to fishery

Table 1 Size of the blue mussel bed areas (km^2) in the Danish Wadden Sea in five zones during 1986–2000

Zone (km^2)	1	2	3	5, 6	7	Sum: 1 + 5, 6	Sum: 2 + 3 + 7
År	Open[a]	Open	Open	Open	Open	Open	Open
1986	2.69	0.19	0.05	>10.0	1.0	12.69	1.94
1991	3.14	4.00	0.54	2.69	0.55	5.83	5.09
1992	3.14	4.00	0.54	–	0.00	>3.14	4.54
1993	3.01	4.00	0.79	0.96	0.91	3.97	5.70
	Closed	Open	Open	Closed	Open	Closed	Open
1994	2.90	2.90	–	0.96	0.91	3.86	3.81
1995	2.90	3.90	0.55	0.96	0.91	3.86	5.36
1996	0.90	2.80	0.40	1.28	0.94	2.18	4.14
1997	3.29	3.60	0.90	1.38	2.11	4.67	6.61
1998	0.80	3.40	2.42	1.38	2.11	2.18	7.93
1999	1.23	3.40	1.10	2.11	1.54	3.34	6.04
2000	1.23	3.40	1.10	2.11	1.54	3.34	6.04
Average 1986-93	3.00	3.08	0.48	>4.55	0.73	>6.41	4.32
Average 1994-00	1.89	3.34	1.08	1.45	1.44	3.35	5.70

From 1994 and onwards the management scheme for mussel fishery was introduced and mussel fishery was allowed in zones 2, 3 and 7, and prohibited in zone 1, 5 and 6. Data for zone 5 and 6 is pooled. Zone 4 and 8 is omitted due to few data.–, no information

[a] Parts of zone 1 was closed after 1982 due to an ecological reference area west of the island Langli (see Fig. 1)

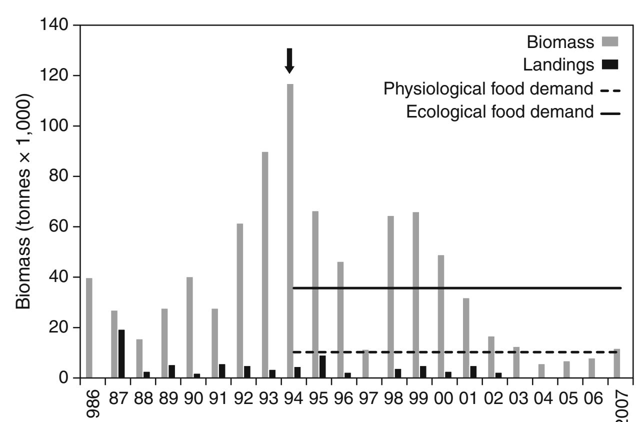

Fig. 2 Total estimated annual blue mussel biomass (metric tonnes) present in the Danish Wadden Sea during 1986–2007 together with the annual mussel landings. From 1994 and onwards, the level of the physiological food requirement and the ecological food requirement for the mussel-eating birds are shown. The *arrow* indicates the year 1994, when the blue mussel management scheme was introduced

decreased from 1994 (closed zones 9,593 tonnes, open zones 8,891 tonnes) to 2007 (closed zones 612 tonnes, open zones 376 tonnes). These changes were statistical significant (Closed zones pooled: $P < 0.02$; $T = -3.01$; DFE = 8. Open zones pooled: $P < 0.01$; $T = -3.85$; DFE = 8. Regression analyses with autoregressive errors).

The annual amount of landed blue mussels varied during 1994–2007 (Fig. 2). The figures for 1994–2002 were in average 2,513 metric tonnes, with the highest amount in 1995 (8,900 metric tonnes), and only 260 metric tonnes in 1997. After 2003, no blue mussels were landed (except for 375 metric tonnes in 2008), either due to a poor mussel quality or a low production, thus no fishing quota was given.

Bird Surveys

The total, average number of eiders counted in the Danish Wadden Sea during winter (October–February) decreased from about 25,000 in 1986/87 to 12,000 in 2007/08 (Fig. 3). Numbers were high and fluctuating during the earliest years, but decreased after 1994. Oystercatcher numbers increased from c. 15,000 in 1986/1987 to more than 40,000 in 2007/2008. Herring gull numbers fluctuated, but were more or less stable during the period at about 17,000 individuals (Fig. 3). Only eiders showed a statistical significant relationship between total annual average numbers and estimated blue mussel biomass in the Danish Wadden Sea (Parameter estimate = 0.116; $T = 2.19$; $P < 0.05$; $R^2 = 0.19$, $N = 20$, regression analysis with auto regressive errors).

Eiders were evenly distributed between zones closed and open to mussel fishery (49.8 vs. 50.2%). However, both oystercatchers and herring gulls occurred in significantly higher numbers in zones open to mussel fishery (59.5 and 62.2%) than in zones closed to mussel fishery (40.5 and 37.8%) (oysterchatcher: $T = 7.14$; $P = < 0.05$; $N_{14,14}$. Herring gull: $T = 4.24$; $P = < 0.05$; $N_{14,14}$, one-way ANOVA, data log-transformed).

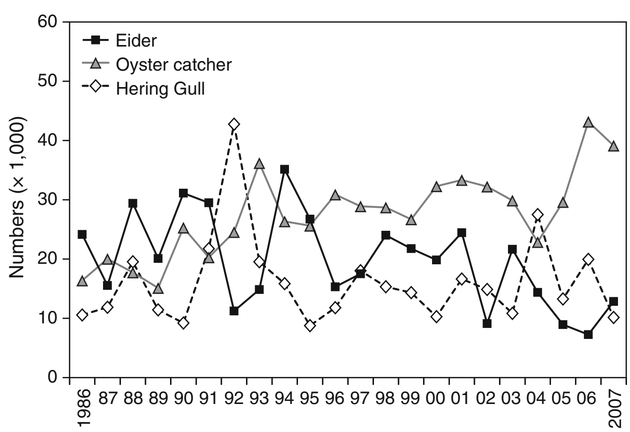

Fig. 3 Average counted numbers of three mussel-eating bird species present in winter (October–February) during 1986 (signifying winter 1986/1987) to 2007 (2007/2008). The overall trend is negative for eider (Parameter estimate = −0.619; $T = -2.69$; $P < 0.05$; DFE = 20), positive for oystercatcher (parameter estimate = 0.840; $T = 5.23$; $P < 0.001$; DFE = 20) and stable for herring gull (parameter estimate = −0.0320; $T = -0.12$; $P = 0.90$; DFE = 20). Regression analysis with autoregressive errors was used

Ecological Food Demands Versus Observed Mussel Stocks

The novel total annual ecological food demand for mussel-eating waterbirds was estimated at c. 35,800 metric tonnes (Table 2). Divided into the species preferred feeding habitats (eiders in the sub-littoral and oystercatcher together with herring gull in the littoral zone) there is a demand of at least c. 26,100 metric tonnes blue mussel to be set-aside for the eiders in the sub-littoral zone and at least c. 9,600 metric tonnes for oystercatcher and herring gull in the littoral zone. Note that the food demands for these two species are not added, since they take mussels from the same habitat where also their interactions occur (e.g. kleptoparasitism), thus they are sharing the same feeding pool. Due to this, the set-aside food demand is estimated for the species with the largest demand to supporting both species. When the estimated physiological food demand from 1994 and the novel ecological food demand from 2008 are compared to the estimated mussel biomass in the Danish Wadden Sea, it appears that the total ecological food demand of c. 35,800 metric tonnes for the mussel-eating birds was only found during 5 years since 1994 (Fig. 2), and after 2000 the annual mussel stocks have not reached this level.

DISCUSSION

The size of the Danish Wadden Sea blue mussel stocks have been highly variable since monitoring started in 1986, and after 1994, when the blue mussel management scheme was introduced, the total blue mussel biomass had decreased continuously. In an attempt to reverse the declining trends in blue mussel abundance, 1,000 metric tonnes of seed mussels were spread out over former mussel beds in zone 4 (open to mussel fishery) in 2002 to re-establish former mussel beds there. However, it has achieved no permanent effect, despite the fact that these mussel beds were not fished (DTU Aqua unpublished data).

Decreases in blue mussel biomass have also been reported from the Schleswig–Holstein and Lower Saxony's Wadden Sea in recent years, although increases in mussel biomass have been reported from the Netherlands Wadden Sea (de Vlas et al. 2005). The reasons for these dramatic fluctuations in the mussel stocks and bivalves in general are

Table 2 Estimation of the physiological and the ecological food demand (metric tonnes blue mussel year^{-1}) for eider, oystercatcher and herring gull

	Eider	Oystercatcher	Herring gull
Number of birddays year^{-1}	6.7×10^6	9.3×10^6	5.2×10^6
Physiological food demand tonnes year^{-1}	10,372	1,246	208
Ecological food demand tonnes year^{-1}	26,138	9,640	1,137
		Sub-littoral mussel beds	Littoral mussel beds
Ecological food demand pr. habitat tonnes year^{-1} (in total 35,778 tonnes year^{-1})		26,138	9,640

The total ecology food demand is divided into the sub-littoral and the littoral zones

not well known, but the annual biomass seems to depend on winter climate, spawning, and settling conditions for the mussel larvae (de Vlas et al. 2005; Beukema et al. 2009). Successful settlement and subsequent growth depends, among other things, on suitable temperatures, sediment type, suitable settlement substrate, moderate competition levels, low predator pressure and abundant phytoplankton on which to feed (Dankers and Beukema 1983; Beadman et al. 2002; Büttger et al. 2008). The milder winter climate of very recent years seems also to reduce recruitment amongst blue mussels and other bivalves (Beadman et al. 2002; Büttger et al. 2008). In addition, storms and other extreme weather conditions are known to remove and even destroy mussel beds (Nehls and Thiel 1993; Steenbergen et al. 2005). Unfavourable conditions caused by one or more of these factors can lead to complete disappearance of mussel beds together with removing entire year-classes, causing dramatic year to year variations in biomass (Steenbergen et al. 2005). Studies in England and The Netherlands have shown that it is difficult to manage blue mussel stocks with the aim of reducing fluctuations and to secure a stable biomass for harvesting, since stocks are liable to major influence from various factors of which only some can be managed externally (Dare et al. 2004; Imeson et al. 2006).

Blue mussel data from the Danish Wadden Sea was scarce before 1994, although they show (for single zones opened and closed to mussel fishery) no significant differences in the biomass before and after 1994, the year that the blue mussel management plan was put into force. After 1994, the mussel biomass decreased in both zones, i.e. those open and closed to mussel fishery. There was a significant decrease in the extent of the blue mussel beds after 1994 in zones closed to mussel fishery, but no change amongst those beds in zones open to fishing. These results show that the mussel fishery does not necessarily reduce available mussel biomass or the extent of the mussel bed areas. In addition, it should be noted, that neither the biomass nor the size of the mussel bed areas increased after 1994 in zones closed to mussel fishing. In other parts of the Wadden Sea, the mussel biomass also decreased, and since the settlement of new mussel cohorts are dependent on severe winter climate, it has been suggested that the warmer winter climate of recent years could contribute to the declining mussel stocks (Büttger et al. 2008).

Annual landings of blue mussel varied, but generally declined after 1994, and from 2004 landing almost ceased. This results show that the mussel management planned has not been able to secure a sustainable fishery for the fishermen. In the Netherlands Wadden Sea the landings of mussels and cockles had also shown large annual variations, but when considered the amount of landed cockles and mussels together they supplement each other and reduce the annual fluctuations in the total amount of shellfish landings (Imeson et al. 2006).

Overall eider numbers were positively correlated with mussel biomass in the Danish Wadden Sea, and since the mussel biomass had decreased after 1994 the eider numbers had followed. On the other hand, the oystercatcher and herring gull numbers were either stable or increased during the study period. Survey results from the entire Wadden Sea show that the three mussel-eating bird species decreased significantly since 1987 (the eiders since 1996), probably due to food limitations caused by an intensive shellfish fishery in the Netherlands Wadden Sea that supported large parts of the total number of mussel-eating birds (Ens 2006; Blew et al. 2005). The bird species feeding habitat differs, while the eiders dive for mussels in the sub-littoral zone (Nehls and Ketzenberg 2002), the oystercatcher together with the herring gull feed on the exposed mussel beds during low tide (Hilgerloh 1997; Ens et al. 1996a, b). The species difference in feeding habitat and the shellfish fishery practice between the Netherlands and Denmark is probably the reason for contrasting trends amongst bird species over time between the two regions. In Denmark only the natural sub-littoral mussel beds are fished (mussel culture lots are not allowed, and thus no fishery for mussel seeds occurs) and cockle fishing is restricted to a small part (<1%) of the littoral zone (Dahl et al. 1994). This contrasts with the Netherlands, where the sub-littoral zone is fished for mature blue mussels together with mussel seeds, and parts of the littoral zone for cockles (Ens et al. 2004). These differences between the Netherlands and Denmark could contribute partially to explaining why the trends in abundance of oystercatcher and herring gull differ between the two countries (Blew et al. 2005). However, both the species depend on the littoral zone, and since no mussel fishery take place in this zone in both countries, a difference could be that parts of the Netherlands littoral zone is fished for cockles, compared to a small cockle fishery in the Danish Wadden Sea. For comparison during 1994–2003, an average of 21,000 metric tonnes of cockles was annually landed in the Netherlands compared to 740 metric tonnes in the Danish Wadden Sea (Essink et al. 2005), suggesting that the larger cockle fishery in the Netherlands Wadden Sea could contribute to the decreasing trends in Oystercatcher and Herring Gull there. Unfortunately, the information on the littoral mussel and cockle stocks is scarce from the Danish Wadden Sea, since most survey effort is focused on the sub-littoral mussel stocks.

In the Netherlands Wadden Sea, a fishery plan was introduced in 1993 as a result of the intensive mussel and cockle fishery of the late 1980s, which resulted in high mortality amongst both eiders and oystercatchers (Smit et al. 1998). The Netherlands fishery plan should re-establish the blue mussel beds and cockles' fields by closing zones (covering 26% of the intertidal area) to mussel fishery and secure enough food for the mussel-eating birds by regulating the annual catch. The results in the Netherlands showed a successful increase in the intertidal blue mussel bed area in the zones closed to mussel fishery. From nearly no intertidal mussel beds between 1990 and 1994, the area had increased to 2500 ha in 2002. For the food set-aside for the mussel-eating birds the results in the Netherlands showed that calculations based on the physiological demand was far to low, and it was recommended to base calculations on ecological food demand (Ens et al. 2004). However, in a later study, Imeson and Bergh (2006) assessed the result of the Netherlands mussel fishery policy and concluded that it had been unable to manage the complex ecosystem satisfactorily, and there is also evidence of more recent mass mortality events amongst shell-fish eating waterbirds, caused by food shortages (Camphuysen et al. 2002).

For the Danish Wadden Sea, the revised estimates including ecological food demands of the mussel-eating birds show that at least c. 35,800 metric tonnes blue mussels annually are necessary to support the birds at a level which is assumed to secure them a favourable conservation status according to the EU Bird Directive and the EU Habitat Directives. This amount is more than three times the amount that was set-aside in the original mussel management scheme. However, diet studies show that the proportion of mussels in the species' diet occasionally can be even higher than those used in our estimations (Hilgerloh 1997; Ens et al. 1996a, b; Smit et al. 1998; Dernedde 1994; Goss-Custard et al. 1996; Hilgerloh 1999; Maagaard and Jensen 1994; Wilkens and Exo 1998; Kubetzki and Garthe 2003), and thus raising the total amount of blue mussels necessary for the species. In addition, the ecological factor used to multiply the physiological food amount to get the ecological food demand is uncertain for both eider (Goss-Custard et al. 2004) and herring gull. For eiders, we have used the lowest factor in the range, due to our assumption that there is little intraspecific competition during feeding, but for oystercatcher we used the highest values. Thus, the revised estimated amount of mussels to be set-aside presented in this paper must be considered as an order of magnitude which is certainly better than the 1994 value, but might be lower that the amounts truly needed by the birds. Hence this can still be improved by more specific studies on the focal species food selection and energetics in the Danish Wadden Sea.

Comparing the revised estimate for the ecological food requirements of the mussel-eating birds, the annual blue mussel production in the Danish Wadden Sea since 1994 has only exceeded the estimated ecological food demand in 6 years, indicating that it may be difficult in the future to manage the mussel stocks in a way that halts the decreasing trend in eider numbers. It is obvious that it is a substantial challenge to manage the blue mussel stocks since the only tool to manage seems to be to regulate fishery intensity, which at least in this study is of minor importance to the changes we have seen in total blue mussel stocks. Since climate and ecological interactions seem to be major factors, it could perhaps be more realistic to establish a flexible management system that took the fluctuations in the blue mussel stocks in account. However, according to both the aim in the Wadden Sea Plan (Essink et al. 2005), and the EU Bird and Habitat Directives, the target for achieving favourable conservation status is for the bird species (e.g. eiders) to attain sufficient feeding opportunities to survive and reproduce, and that their numbers are stable or increasing.

The results we found are opposite to the assumptions put forward about the effect of the mussel management scheme from 1994 for the Danish Wadden Sea, and it is concluded that the management has not been able to increase or stabilize the blue mussel biomass, to re-establish blue mussel beds in zones closed to mussel fishery, nor to prevent eiders numbers decreasing. Thus, it seems reasonable to recommend a revision of the mussel management scheme for the Danish Wadden Sea, to continue and improve mussel stock and bird surveys, and to consider novel studies of the mussel-eating birds energetics for improved set-aside estimates and future assessments.

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AUTHOR BIOGRAPHIES

Karsten Laursen (✉) is a senior adviser doing research in avian ecology and assessment of human exploitation of wetland habitats, especially interactions between bird species and their local food systems.
Address: National Environmental Research Institute, Department of Wildlife Ecology and Biodiversity, University of Aarhus, Grenåvej 14, 8410 Rønde, Denmark.
e-mail: kl@dmu.dk

Per Sand Kristensen is a senior adviser and consultant in shellfish fishery and aquacultures, doing research in the balances of fertilizers and the role of mussels as suspension feeders together with assessment of natural stocks of mussels.
Address: DTU-Aqua, Section for Coastal Ecology, Technical University of Denmark, 2920 Charlottenlund, Denmark.
e-mail: psk@aqua.dtu.dk

Preben Clausen is a senior researcher, whose main research fields are population dynamics, nutritional ecology and energetics of waterbirds (geese, swans and ducks) together with optimal management of wetlands.
Address: National Environmental Research Institute, Department of Wildlife Ecology and Biodiversity, University of Aarhus, Grenåvej 14, 8410 Rønde, Denmark.
e-mail: pc@dmu.dk